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STABLE POPULATION SELECTION

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by

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Abstract

A simple model is developed to describe population selection in an ecological system. Stable populations are characterized, and some existence theorems are given.

The purpose of this paper is to describe the growth of stable populations in isolated environments. The meaning of this statement will shortly be made precise; the motivation of the problem can be appreciated through the following situation.

Imagine a stretch of seashore immediately following an exceptionally violent storm. Along this stretch of coast are a number of tide-pools; isolated environments of rock and sand and sea water, swept clean of life by the exceptional violence of the recent storm. All of these tide pools are virtually identical as potential habitats for various forms of coastal life.

Now imagine the same stretch of shore after some suitably long time, say a year, has elapsed. Each tide pool now contains a diverse population of living organisms, co-existing with each other in the same environment. Furthermore, it is likely that some, if not all, of the organisms in a particular tide pool can be classified as permanent residents; that is, over a period of many tides, these organisms remain part of the population of that tide pool.

Looking at another tide pool, there is no reason to expect that the population of organisms which it supports will be identical to that of the first. On the contrary, it is likely that two different tide pools, while sharing the same physical characteristics, will support populations of markedly different composition.

This difference in population among physically identical tide pools is due, presumably, to the different sequences in which organisms are introduced to each tide pool by the random action of the tides. The introduction of an organism to a tide pool changes the characteristics of that environment as a potential habitat for other organisms; and

different organisms change the environment differently. Thus the environment associated with each tide pool undergoes a process of evolution as new organisms are introduced by the tide.

This is not to imply that the first organisms to be introduced to a particular tide pool will of necessity become permanent residents of that pool; they may be displaced by later arrivals. The dynamics of this process is one of the things which we hope to study by means of a formal model. We will also want to characterize the degree and manner in which this dynamic process becomes stable over time.

The Model

Let $\mathcal{O}$ be the (finite) universe of organisms, and let $\mathcal{H}$ be the set of available habitats. For most of what follows, we will consider only a single habitat H.

Let R be a binary relation defined on $\mathcal{O}$ such that for all organisms x in $\mathcal{O}$ the statement xRx is false (i.e., ~ xRx). The relation R is called "prevents", and if for organisms x, y in $\mathcal{O}$ xRy then we say that (the presence of) x prevents y (from occupying the same habitat).

The relation R is not, in general, symmetric. That is, it may be that for some organisms x and y in $\mathcal{O}$ xRy but ~ yRx. (To see that this is reasonable, replace "prevents" with "preys on" so that xRy reads "x preys on y".)

A collection of organisms x, y, ..., z such that xRyR ... RzRx is called a cycle. A cycle is called even or odd, depending on whether the number of organisms in it is even or odd.

Time is divided into periods, and in each period at most one organism can be introduced to each habitat. (Allowing many organisms to be introduced simultaneously would not change the results, but would needlessly complicate the presentation.) The population of a habitat H at the end of period n

will be written $Pn(H)$, or, when no confusion will result, Pn. We assume that $Po=\phi$, the empty set, and for all periods n, Pn is of course a subset of $\mathcal{O}$. We further assume that the length of each period is short compared to the life-span of the organisms in question.

For each organism x in $\mathcal{O}$ define $D(x)=\{y\epsilon\mathcal{O}|xRy\}$. $D(x)$ is thus the set of all organisms y which are prevented from occupying the same habitat as the organism x. For each population P (that is, for each subset of $\mathcal{O}$) define $D(P)\equiv\bigcup_{x\epsilon P}D(x)$. $D(P)$ is the set of organisms y which are prevented from occupying the same habitat as some organism x in the population P. Finally, let $U(P)\equiv\mathcal{O}-D(P)$. $U(P)$ is the set of all organisms which are <u>not</u> prevented from occupying the same habitat as any organism in the population P.

The population Pn of a habitat H at the end of period n evolves in the following way. If no new organism is introduced into the habitat at the start of period n+1, then $Pn+1=Pn$, that is, the population is unchanged.

If, at the start of period n+1, an organism x is introduced into the habitat such that $x\epsilon D(Pn)$, then $Pn+1=Pn$. That is, if a new organism x is introduced into the habitat, such that x is prevented from occupying the same habitat as one of the organisms already in the population of that habitat, then the organism x is eliminated, and the population remains unchanged.

If, at the start of period $n+1$, an organism x is introduced such that $x \in U(Pn)$ (i.e. $x \notin D(Pn)$), then $Pn+1=Pn \cup \{x\}-D(x)$. That is, if the new organism x is not prevented from occupying the habitat by any member of the existing population of that habitat, then x occupies a place in the habitat. Any organism prevented from occupying the same habitat as x is then eliminated from the population.

Analysis of the Model

The first question which we must answer is which populations are <u>feasible</u>, that is, for which subsets P of $\mathcal{O}$ is it possible that $P=Pn(H)$ for some habitat H at the end of some period n?

<u>Lemma 1</u> A population P is feasible if and only if $P \subseteq U(P)$.

<u>Proof</u>: If $P \nsubseteq U(P)$, then there are elements $x, y \in P$ such that xRy. If $x \in U(P)$, then once x has entered the habitat, y is eliminated; otherwise, there is an element z in P such that zRx, and x is thus eliminated.

If $P \subseteq U(P)$ and P has p elements, then if the elements of P are the first to be introduced to H, $P=P_p(H)$.

We also want to consider conditions which will insure that a subset of a given population is <u>permanent</u>; i.e., conditions which imply that if $P \subseteq Pn$ for some n, then $P \subseteq Pm$ for all $m \geq n$.

<u>Lemma 2</u> A feasible population P is permanent if $P \subseteq U(U(P))$

<u>Proof</u>: Suppose $P \subseteq Pn$ for some n. The only way some $x \in P$ might be displaced is if some y is introduced to the habitat such that yRx. But $P \subseteq U(U(P))$, so the fact that yRx implies that $y \in D(P)$, and thus $y \in D(Pn)$. So $P \subseteq Pn=Pn+1$, and by induction, $P \subseteq Pm$ for $m \geq n$.

We shall often denote the set $U(U(P))$ by $U^2(P)$, and say that the set $U^2(P)$ is the set protected by the population P. This terminology is meant to reflect the fact that any organism which prevents a member of $U^2(P)$ is in turn prevented by some member of P. A population P such that $P \subseteq U^2(P)$ will be called self protecting, and, as shown above, we see that self protecting populations are permanent.

In order to talk about stability, we must investigate the way in which permanent populations grow into larger permanent populations. Consider a population P such that $P \subseteq U(P)$ and $P \subseteq U^2(P)$, but $P \neq U^2(P)$. P is feasible and self protecting and hence is permanent.

Consider now an organism x in $U^2(P)-P$, and some other organism z such that zRx. Since x is protected by P, there is a member of P which prevents z. Thus no organism z which prevents x can ever become part of some population which contains the population P. Therefore, if at any period the organism x is introduced to a habitat with a population Pn which contains P, then the organism x occupies a place in that habitat. Furthermore, every population $Pm (m \geq n)$ contains $P \cup \{x\}$; that is the popula- $P \cup \{x\}$ is a permanent part of the population.

We say, therefore, that a feasible, self protecting population is stable when it has grown to the point where it includes all organisms which it protects. Thus a stable population P is one such that $P=U^2(P) \subseteq U(P)$.

Theorem 1: There exists a stable population for every set of organisms $\mathcal{O}$ and every binary relation R.

This theorem, which is proved as a corollary in Roth [1975], does not preclude the possibility that the empty set is a stable population, and possibly the only one (see example 4). But the empty set is only

stable in the absence of some organism which is unprevented by any other organism. That is:

<u>Lemma 3</u>: The empty set is a stable population if and only if the set $U(\emptyset)$ is empty.

<u>Proof</u>: The empty set prevents nothing, and thus $U(\phi)=\emptyset$, and $U^2(\phi)=U(\emptyset)$. If $U^2(\phi)=\phi$, then ϕ is a stable population, otherwise not.

The fact that circumstances exist under which even the empty set is a stable population serves to emphasize that the kind of stability we are talking about here is dynamic rather than static. Before we go on to consider what manner of static equilibrium can occur, let us describe the dynamics associated with a stable population.

Consider a habitat containing a stable population $P=Pn$. We may think of the set of all organisms as being partitioned into three sets; P, $D(P)$, and $U(P)-P$. For convenience we shall call the third set P^1.

If a member of $D(P)$ is introduced into the habitat, it is, of course, immediately eliminated. If a member x of P^1 is introduced into the habitat, however, it becomes part of the population $Pn+1$, since it is contained in $U(Pn)$. However, x is unprotected by P, which means that there is an organism y in $U(P)$ such that yRx. Since this organism y is not in P, it must be in P^1. Thus, unless xRy, x will be eliminated from the population if y is introduced into the habitat.

Therefore the population of this habitat over subsequent periods will consist of the permanent population P, augmented by some transient organisms from P^1.

Since stable populations are permanent, the population of any given habitat will tend towards the largest stable population compatible with its present population. Under suitable circumstances, this can lead to a stable population P such that the set P^1 is empty. In this case P=U(P), and we say that P is <u>completely stable</u>. Any organism introduced into a habitat containing a completely stable population is immediately eliminated, since any organism outside of P is in D(P). (It is clear that a completely stable population is stable, since if P=U(P), then $P=U^2(P)$). Note that a completely stable population is never empty.

The mathematical structure associated with completely stable populations has been studied in other contexts. In the study of cooperative games, such structures are called <u>solutions</u>; and in the study of graphs they are called <u>kernals</u>. It is well known that a given universe $\mathcal{O}$ and binary relation R (which can be viewed as a graph), may admit a multiplicty of completely stable populations (see example <u>1</u>), or none at all (see example <u>2</u>).

The following sufficient condition for at least one completely stable population to exist is due to Richardson [1953].

<u>Theorem 2</u>: If there are no odd cycles (for a given $\mathcal{O}$ and R) then there exists a completely stable population.

One of the things we wish to be able to determine is when a given set of data; i.e. the observed populations of a set of isolated habitats H, is consistent with the hypothesis that these populations are completely stable with respect to some (perhaps unknown) relation R. Obviously, a necessary condition is that, for each habitat H in $\mathcal{H}$, Pn(H)=Pn+1(H).

The following theorem gives a necessary and sufficient condition which involves only observations from one period. It is proved in Wilson [1972].

<u>Theorem 3</u>: The data Pn(H) for each H in $\mathcal{H}$ is consistent (with the above hypothesis) if and only if for each habitat H, and each subset $\mathcal{S}$ of H, $Pn(H) \subseteq \cup_{S \in \mathcal{S}} Pn(S)$ only if $Pn(H) \supseteq \cap_{S \in \mathcal{S}} Pn(S)$.

Examples

In the accompanying diagrams, organisms are indicated by letters and the relation R by arrows. An organism is thus connected by arrows to all those organisms which it prevents.

<u>Example 1</u>: (See Figure 1). In this example, the following populations are stable: ϕ, {a,c}; {a,c,e,g}; {a,c,f,h}; and {b,d,f,h}. Of these the last three are completely stable.

<u>Example 2</u>: (See Figure 2). In this example, the sole stable population is {a}, which happens to be equal to $U(\mathcal{O})$. No completely stable populations exist.

<u>Example 3</u>: (See Figure 3). In this example, the sole stable set is {a,c}, which is completely stable. This demonstrates that the sufficient condition of Theorem 2 is not necessary to insure the existence of completely stable sets.

<u>Example 4</u>: (See Figure 4). In this example, the empty set is the sole stable population. Naturally, it is not completely stable.

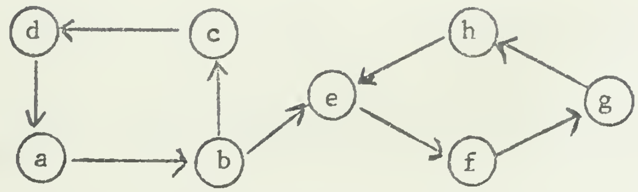

Figure 1

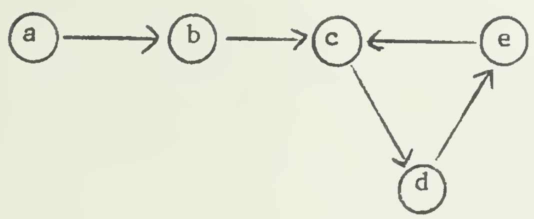

Figure 2

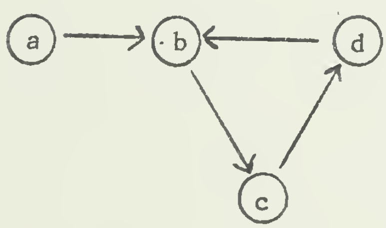

Figure 3

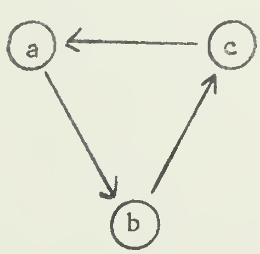

Figure 4

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